Gross Efficiency in Cyclic Sports

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Chapter 1

General introduction

Mechanical power output (PO) produced during cycling, speed skating, running or any of the primary cyclic propulsive activities can be described as the complex interplay between the physiological factors presented in the Joyner model[1] (Figure 1.1). Four physiological parameters are of great importance to allow an individual to deliver exceptional athletic performances: 1) the maximal oxygen uptake ($\dot{V}O_{2max}$), 2) oxygen uptake ($\dot{V}O_2$) at the ventilatory threshold ($\dot{V}O_2$@VT), 3) the anaerobic capacity, and 4) the ability to convert the aerobic and anaerobic energetic resources (1-3) to forward propulsion, the gross efficiency (GE).[1,2] The first three physiological parameters have been extensively studied. It seems that the ability of humans to produce metabolic energy (anaerobically and aerobically) may be approaching the species limits, and therefore much of the ability to improve performance by directly increasing metabolic power production (power input (PI)) may have already been achieved.[3,4] Accordingly, in the absence of reductions in power losses due to technological innovations, performance improvements are reasonably related to the ability to improve GE.[4] For example, the latest remarkable improvement in speed skating performance has been due to an improvement in GE.[5,6] The introduction of the klapskate resulted in a significantly higher GE, namely 16.3% instead 14.8% with conventional skates, which increased the PO that could be delivered by the skaters, while producing the same amount of metabolic energy.[7]

Metabolic energy production

In order to perform exercise the body continuously needs chemical energy, which is derived from high energy phosphate compounds, predominantly phosphocreatine (PCr) and adenosine triphosphate (ATP). When this high energy phosphate (~P_i, inorganic phosphate) is split from these compounds, free energy (ΔG) is released and can be used to perform biologic work, for example the actin-myosin binding and conformational changes that are central to muscle contraction.[8] The reaction by which energy is released from high energy compounds can be described by Equation 1.1 and Equation 1.2:[9]

$$PCr + ADP \leftrightarrow ATP + Cr \qquad \text{Equation 1.1}$$

$$ATP + H_2O \leftrightarrow ADP + P_i + \Delta G^{\circ\prime} \qquad \text{Equation 1.2}$$

The change in free energy, ΔG, differs between reactions, therefore ΔG°' describes the standard free energy change (7.3 kCal·mol^{-1} or 30.6 kJ·mol^{-1}).[9] Given that stored high energy phosphate compounds are not plentiful, these compounds need to be continuously regenerated during exercise at a rate that approximates the energy expenditure of the exercise task. The anaerobic and aerobic metabolism of carbohydrates and fatty acids (amino acids are only used as a substrate during starvation) serves to regenerate ATP from ADP and P_i.[8]

Anaerobic energy metabolism

Short, sprint like, competitive events (for example the individual sprint during track cycling or the 500 m speed skating) heavily rely on anaerobic energy production, because the kinetics of aerobic energy production are relatively slow and the maximal rate of aerobic energy production is too low to account for the magnitude of muscular power output during sprint activities.[10,11] Anaerobic energy metabolism is also very important during the start of submaximal exercise, before the external respiration adequately meets the muscle respiration and $\dot{V}O_2$ reaches a steady state. There are two main anaerobic sources to regenerate ~P_i; PCr hydrolysis and glycolysis.[8]

Substrate level phosphorylation from PCr hydrolysis is the primary source of ATP resynthesis during the first several seconds of high intensity exercise,[12] which is due to the high activity of the enzyme creatine kinase, which catalyzes the reaction from PCr and adenosine diphosphate (ADP) to ATP and creatine (Cr) (Equation 1.1). The maximum rate of ATP resynthesis by PCr hydrolysis is four to eight times the rate of ATP resynthesis by aerobic energy metabolism.[8] Glycolysis (glucose catabolism), and in particularly glycogenolysis is important beyond the first few seconds of high intensity exercise. Glycogenolysis is the glycogen catabolism to glucose-6-phosphate, the product of the first step of glycolysis. Glycogen phosphorylase, the enzyme that determines the maximal rate of glycogenolysis, is stimulated by the metabolic byproducts from PCr hydrolysis.[12] Thus, when PCr stores become depleted, glycolysis is stimulated.

Anaerobic glycolysis results in the formation of 2 pyruvate molecules and 2 ATP molecules, as is described in Equation 1.3. However, when glycogen provides a glucose molecule for anaerobic glycolysis this results in a net gain of 3 ATPs, instead of 2.[8] The enzyme phosphofructokinase is probably the rate limiting enzyme of glycolysis during maximal exercise.[8] Continuous anaerobic metabolism involves constant NAD^+ regeneration from NADH. When pyruvate production exceeds pyruvate oxidation, pyruvate combines with hydrogen, resulting in the formation of lactate, facilitated by lactate dehydrogenase (Equation 1.4).[8] In this way NAD^+ can be regenerated and anaerobic glycolysis can proceed. PCr depletion and high blood and muscle lactate concentrations eventually result in fatigue and the cessation of exercise, which is why it has been suggested that there is a maximum to the amount of ATP that can be resynthesized anaerobically, the anaerobic capacity.[13] When exercise continues for more than ~1-2 min, aerobic metabolism becomes the major ATP producing system.[10]

$$glucose + 2P_i + 2ADP + 2NAD^+ \rightarrow 2pyruvate + 2ATP + 2NADH + 2H^+ + 2H_2O \quad \text{Equation 1.3}$$

$$glucose + 2P_i + 2ADP \rightarrow 2lactate + 2ATP + 2H_2O \quad \text{Equation 1.4}$$

Aerobic energy metabolism

Under conditions of high mitochondrial enzyme activity and when oxygen is available, pyruvate produced during anaerobic glycolysis is irreversibly converted to acetyl-CoA (Equation 1.5), which enters the citric acid cycle (in the mitochondrial matrix) for aerobic energy metabolism.[8] The enzyme complex pyruvate dehydrogenase catalyzes the decarboxylation of pyruvate into acetyl-CoA. Beta oxidation of fatty acids also results in the formation of acetyl-CoA in the mitochondrion.[8] Within the citric acid cycle the acetyl unit of acetyl-CoA is broken down to two molecules of carbon dioxide and four pairs of hydrogen atoms (Equation 1.6).[9] During the oxidation of the acetyl unit the four pairs of high energy electrons are transferred to 3 NAD^+ and 1 FAD molecule (Equation 1.6).[9]

The passage of electrons from NADH and $FADH_2$, produced during glycolysis, beta oxidation, and the citric acid cycle, to oxygen in the electron transport chain (or respiratory chain) results in a proton gradient across the inner mitochondrial membrane. This membrane potential results in a proton flow across the membrane which drives the oxidative phosphorylation of ADP to ATP.[8]

$$pyruvate + NAD^+ + CoA \rightarrow acetylCoA + CO_2 + NADH^+ + H^+ \quad \text{Equation 1.5}$$

$$acetylCoA + 3NAD^+ + FAD + GDP + P_i + 2H_2O \rightarrow 2CO_2 + 3NADH + FADH_2 + GTP + 2H^+ + CoA \quad \text{Equation 1.6}$$

The citric acid cycle (or tricarboxylic acid (TCA) cycle or Krebs cycle), electron transport chain and oxidative phosphorylation are the three main components of aerobic metabolism, which is a relatively slow process, but results in the net production of 32 ATP molecules from the complete breakdown of glucose.[8] In contrast, only 2 ATP molecules are generated during glycolysis, the first stage of glucose degradation. The complete breakdown of one triacylglycerol molecule results in the formation of 460 ATP molecules.[8]

Metabolism (enzyme activity of the rate limiting enzymes that control metabolism) is stimulated by a decrease in the ATP/ADP and intra-mitochondrial $NADH/NAD^+$ ratio, which occurs at the start of exercise. Both ADP and NAD^+ need to be available for energy metabolism to continue. NAD^+, but also FAD, is regenerated in the electron transport chain, in order to continue aerobic energy metabolism. This kind of feedback mechanism is necessary to maintain adequate energy availability.[8]

Measuring metabolic energy production

Whole-body metabolic energy production by anaerobic and aerobic ATP forming processes during rest and exercise can be measured using two different methods, direct and indirect calorimetry.

Direct calorimetry

The method of direct calorimetry is based on the law of conservation of energy, which holds that the total amount of energy of an isolated system remains constant. Applied to the living human body, this means that the potential energy from food consumption must equal the external work delivered during exercise, the energy losses through heat radiation from the body, the potential energy in excreta, and the change in energy stores in the body during the same time frame.[14] Using the method of direct calorimetry, requires a subject to live for several hours to days in a large airtight, insulated chamber, i.e. the calorimeter, with a known volume of water circulating through pipes inside the chamber, which absorbs the heat radiated by the subject. The airflow in and out of the chamber needs to be tightly controlled for volume and temperature. Additionally, the income of food and drinks and outgo of excreta needs to be regulated. By using a dynamo, the amount of work done during bicycle exercise, is determined from the heat produced by an incandescent lamp, which is also given off to the water circulating through pipes inside the chamber. In this way, total heat production by the human body is determined from the mass of the water and the increase in temperature of the water and the heat necessary to vaporize the excess water in the expired air leaving the chamber.[14] With this method the metabolic energy production is determined from the total heat produced by the human body. It might be clear that this method is cumbersome in evaluating athletes like cyclists, speed skaters, and runners and is not particularly useful for situations when the rate of energy production is changing dynamically.

Indirect calorimetry

The method of indirect calorimetry is based on the assumption that all ATP producing reactions in the human body eventually rely on the use of oxygen.[8] So, by measuring oxygen consumption during rest or steady state exercise (only under steady state conditions does gas exchange measured at the lungs reflects gas exchange in the cell)[8] the amount of metabolic energy production is determined. It has been shown that the difference between direct and indirect calorimetry is generally below 1%.[8] In the studies described in this thesis gas exchange was measured using open circuit spirometry.

Efficiency

Someone's whole-body efficiency determines the amount of PO or speed that can be generated from the anaerobic and aerobic metabolic energy produced. As efficiency may be different for anaerobic and aerobic ATP resynthesis,[15,16] the efficiency that is described in this thesis is based on measurements of aerobic metabolism. Efficiency is thus only determined when $\dot{V}O_2$ is in steady state and the respiratory exchange ratio (RER) is at or below 1.0. This applies to exercise intensities below the ventilatory threshold (VT), the exercise intensity at which minute ventilation ($\dot{V}E$) starts to increase disproportionately with $\dot{V}O_2$.[8]

The most widely used definition of whole-body efficiency is GE,[17–19] which is the ratio between the mechanical PO and the metabolic power input (PI)[18,20] expressed as a percentage (Equation 1.7).

$$GE = \frac{PO}{PI} \cdot 100 \qquad \text{Equation 1.7}$$

The metabolic PI can be calculated by multiplying steady state $\dot{V}O_2$ (expressed in $L \cdot s^{-1}$) by the oxygen equivalent (O_2eq), based on the respiratory exchange ratio (RER),[21] as described in Equation 1.8.

$$PI = \dot{V}O_2 \cdot (4940 \cdot RER + 16040) \qquad \text{Equation 1.8}$$

Other definitions of efficiency used in the literature include net efficiency, work efficiency, and delta efficiency, all of which rely on baseline subtractions.[18] Baseline measures of energy expenditure, at rest or during unloaded cycling, are subtracted from the total amount of energy expended during exercise to calculate net and work efficiency, respectively. Delta efficiency is defined as the increment in PO divided by the increment in PI between two exercise bouts. Baseline subtractions have been seriously criticized in the literature.[22–24] The main argument against baseline measures is that it assumes that the amount of energy used related to the baseline is constant, independent, and isolated from the energy needed to perform work.[18] Stainsby et al.[22] concluded from their review that baselines do change with increasing PO. For example the energy cost of ventilation increases with exercise intensity.[25,26] Based on this main criticism it can be concluded that the best definition of whole-body efficiency seems to be GE.[17,18,20]

Joyner and Coyle[1] reported in their review on endurance performance that GE, in endurance trained cyclists cycling at 300 W, varies between 18.5% and 23.5%. Reasonably, GE will be lower than the muscle efficiency, which is the product of the phosphorylative coupling efficiency and the contraction coupling efficiency.[27] In which the phosphorylative coupling efficiency is reflected by the ratio between the ATP molecules formed (and the caloric equivalent of ATP) and the number of half-molecules of O_2 consumed (P/O ratio). The amount of free energy (ΔG) from ATP hydrolysis used to deliver work determines the contraction coupling efficiency.[27] The overall muscle efficiency is predicted to be ~30%.[22,28,29]

In order to correctly determine GE the amount of mechanical PO delivered by the athlete needs to be accurately measured. Cycling exercise is extremely suitable for this, because PO can be precisely measured. Therefore the studies described in *Chapters 2-6* made use of cycling exercise.

The energy flow model for cycling

Energy flow models have been used to simulate athletic performances and to study the effect of pacing strategies,[30–33] equipment, and different environmental conditions[4,19,34–36] on performance. In the model momentary performance (e.g. velocity) is the result of the dynamic balance between power production and power dissipation (Equation 1.9).[20,33] Power production (Equation 1.10) consists of the aerobic and anaerobic energy production pathways corrected for GE. The power dissipation side of the model consists of the power losses to overcome different frictional forces. In cycling the frictional forces that need to be overcome are rolling- and air friction.

$$\frac{dE_{cb}}{dt} = PO - PF \qquad \text{Equation 1.9}$$

Equation 1.9 describes the energy flow model, in which PF is the power dissipated to overcome frictional forces, and $\frac{dE_{cb}}{dt}$ is the change in kinetic, rotational and potential energy of the cyclist-bicycle system (*cb*). In cycling on level ground, $\frac{dE_{cb}}{dt}$ averaged over multiple revolutions, is predominantly determined by the rate of change of kinetic energy of the cyclist-bicycle system center of mass, as described in Equation 1.11,[33] in which m is the mass of the cyclist-bicycle system and v is cycling velocity.

$$PO = P_{aer} + P_{an} \qquad \text{Equation 1.10}$$

$$\frac{dE_{cb}}{dt} = \frac{d\left(\frac{1}{2}\cdot m\cdot v^2\right)}{dt} = m \cdot v \cdot \left(\frac{dv}{dt}\right) \qquad \text{Equation 1.11}$$

PO consists of the mechanical power aerobically produced (P_{aer}) and the mechanical power anaerobically produced (P_{an}). P_{aer} can be determined from measurements of $\dot{V}O_2$, including $\dot{V}O_2$ kinetics and $\dot{V}O_{2max}$, O_2eq and GE, as described in Equation 1.12.[37] When applying Equation 1.12, it is assumed that a RER above 1.0 is due to non-metabolic $\dot{C}O_2$ production caused by bicarbonate buffering of lactate, therefore when RER exceeds 1.0, it is presumed that RER equals 1.0.[11]

$$P_{aer-max} = \dot{V}O_{2max} \cdot O_2eq \cdot GE \qquad \text{Equation 1.12}$$

$$P_{aer} = P_{aer-max} \cdot \left(1 - e^{-\lambda t}\right) \qquad \text{Equation 1.13}$$

The kinetics of P_{aer} are described in Equation 1.13, $P_{aer-max}$ is the maximal aerobic power, λ is the aerobic rate constant, and t is time.[33] Equation 1.13 has been used in modeling studies, were the exercise duration is relatively short and exercise intensity is (supra)maximal.[33,37] When endurance exercise is performed at an intensity around the lactate threshold or VT, $\dot{V}O_2$ shows a late (i.e. secondary) increase, the $\dot{V}O_2$ slow component.[38,39] In that case, $\dot{V}O_2$ and thus P_{aer} should be modeled using two exponential terms.[39] P_{aer} is the mechanical equivalent of PI, when there is no anaerobic energy component. P_{an} can be calculated by subtracting P_{aer} from PO[40] and is described by the mono-exponential Equation 1.14.[31,37]

$$P_{an} = P_{an-max} \cdot e^{-\gamma \cdot t} + P_{an-con} \qquad \text{Equation 1.14}$$

P_{an-con} is the asymptotic value reached,[11] P_{an-max} is the maximal anaerobic power at t = 0 s minus the value of P_{an-con}, and γ is the anaerobic rate constant.

The power dissipation side of the model consists of the power needed to overcome rolling frictional forces (F_{roll}) and air frictional forces (F_{air}), as described in Equation 1.15.[33]

$$PF = P_{roll} + P_{air} \qquad \text{Equation 1.15}$$

P_{roll} is dependent on μ the rolling friction coefficient, N the normal force, and *v* (Equation 1.16).[33]

$$P_{roll} = \mu \cdot N \cdot v \qquad \text{Equation 1.16}$$

The largest component of the power dissipation side of the model is P_{air} (Equation 1.17):

$$P_{air} = \frac{1}{2} \cdot \rho_0 \cdot A_p \cdot C_d \cdot {v_{air}}^2 \cdot v \qquad \text{Equation 1.17}$$

in which ρ_0 is the air density, A_p is the frontal area projected to the air, C_d is the dimensionless drag coefficient related to streamlining, v_{air} is the velocity of the air with respect to the body, and *v* the velocity of the cyclist with respect to the ground.[31,33] During indoor races, when there is no wind, v_{air} and *v* are similar.

Critical, but unproven, assumptions regarding gross efficiency

Although the above described model for cycling and the energy flow model for speed skating have been extensively used to simulate athletic performances,[e.g.4,33,37] there are several assumptions, regarding GE, which underlie the energy flow model. The *first assumption* is that GE, determined during submaximal exercise, is constant during the day. The *second assumption* holds that GE is independent of the altitude above sea level at which exercise is performed. The *third assumption* is that GE determined at submaximal exercise intensities is representative of GE at maximal and supramaximal exercise intensities. The final and *fourth assumption* is related to the third one and implies that GE remains constant during fatiguing exercise. To summarize, the goal of this thesis was to try to test these assumptions, which underlie the current version of the energy flow model and, if necessary, to improve the model.[31,33]

As has been described above, the first chapters of this thesis concentrate on GE during cycling exercise (*Chapters 2-6*), as the mechanical PO a subject needs to deliver can be set or easily quantified. However, the same assumptions underlie the energy flow model for speed skating. Unfortunately, it is more difficult to determine PO during speed skating, due to difficulties in quantifying PO and with skating at a submaximal intensity without a RER > 1.0. Therefore, the final studies presented in this thesis (*Chapter 7A* and *7B*) will focus on the fourth assumption regarding GE, not by directly determining GE, but by studying kinematic characteristics of the speed skating technique during races. It is thought that the effectiveness of the push-off (i.e. the direction of the push-off),[41,42] reflected by a small *e*, the angle between the push-off leg and the horizontal, is related to skating efficiency.[43] Unfortunately it is, thus far, impractical to test this hypothesis, due to the above described difficulties. Therefore, studying *e* during races will provide us the best information about changes in GE during speed skating events.

Thesis outline

Chapter 2 – Factors that affect measuring gross efficiency in cycling

Although cycling efficiency has been extensively studied,[44–50] there is little standardization in the methodology of determining GE. Therefore, the effect of stage duration, relative exercise intensity, work capacity (e.g. peak power output attained during a maximal incremental exercise test), and prior maximal exercise on GE was studied.

Chapter 3 – A reliability study

In order to draw correct conclusions from GE measurements, a reliability study had to be performed. What is the smallest difference in GE that can be perceived? And is it necessary to determine an individuals' efficiency every occasion at the same time of the day? There is a circadian rhythm in for example body temperature, but is there a circadian rhythm in gross efficiency? This chapter describes a study in which the between and within day variation in GE was assessed.

Chapter 4 – How to measure anaerobic capacity?

The most widely used method to determine anaerobic capacity has been the maximal accumulated oxygen deficit (MAOD) method, as introduced by Medbø et al.[13] Besides using the MAOD method to determine anaerobic capacity and the relative contribution of the anaerobic energy system to performance, the GE method introduced by Seresse et al.[40] has been used in the literature.[11,37,51,52] However, it was unknown how these two methods related to each other, so the goal of this chapter was to unravel the methodological issues when using the MAOD method (*4A*) and to compare the MAOD and GE method in determining anaerobic capacity (*4B*).

Chapter 5 – Gross efficiency at sea level and at simulated altitude

Cycling and speed skating events are regularly performed at low to moderate altitudes. It is well known that hypoxia reduces air density and therefore air friction and $\dot{V}O_{2max}$, but does hypoxia also influence GE? In this chapter GE was determined during steady state submaximal exercise at sea level and at acute simulated altitude (hypobaric chamber).

Chapter 6 – Estimating gross efficiency during and after high intensity exercise

GE can only be estimated validly during steady state submaximal exercise, because of the unknown anaerobic contribution when exercise is performed above VT.[20] The current version of the energy flow model therefore assumes that GE, determined during submaximal exercise, is representative of GE during (supra)maximal exercise. The goal of *Chapter 6* is to describe a new approach to estimating GE during and immediately after high intensity exercise (*6A*) and apply this new methodology to more sport specific events, i.e. time trial exercise (*6B*).

Chapter 7 – The association between changes in speed skating technique and changes in skating velocity during World Cup races

Chapter 7 tries to gain insight into the cause of changes in speed skating velocity during races, by studying changes in kinematic characteristics of the speed skating posture/technique and by relating these changes in kinematic characteristics to changes in skating velocity (*7A*). *Chapter 7B* evaluates if skating event, sex, and performance level influence the association between changes in the different kinematic characteristics and skating velocity. Changes in knee angle and trunk angle will mainly affect the power dissipation side of the model (Equation 1.9) and changes in e will influence the power production side. Therefore, information about the changes in kinematic characteristics and their relationship with changes in skating velocity will provide us insight into the cause of changes in speed skating velocity during races.

Chapter 8 – General discussion

This final chapter will discuss the validity of the different assumptions regarding GE, will provide an adapted version of the energy flow model, directions for future research, and summarizes the practical applications deduced from this thesis.

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